CHAPTER 1

# Introduction

Ecosystems are paradigmatically among the most complex systems known to science. They contain many different components (e.g., individuals within species populations, species within communities) interacting directly and indirectly in highly interconnected networks (Paine 1980; Schoener 1993; Brown 1995; Yodzis 1995; Levin 1998; Cohen et al. 1990). Moreover, system properties such as trophic structure and functions such as nutrient fluxes and productivity emerge from direct and indirect interactions among the component parts (Brown 1995; Levin 1998). This feature of ecosystems fascinates those who have purely academic interests to develop broad theoretical principles that explain the emergence of complexity (e.g., Holland 1992; Cowan, Pines, and Meltzer 1994; Gell-Mann 1994; Brak 1996; Milo et al. 2002). Complexity theorists, however, treat ecosystems merely as powerful metaphors and accordingly abstract much ecological detail (e.g., treating species as nodes in a network abstracts species' functional traits) to facilitate pattern identification and comparison among myriad physical, chemical, biological, social, and economic systems.

Ecologists too have a fundamental academic interest in resolving ecological complexity (e.g., May 1973; O'Neill et al. 1986; MacMahon et al. 1987; Allen and Hoekstra 1992; Levin 1992, 1998; Turchin 2003). But, that academic interest is tempered by the important practical reality that ecology is increasingly being called upon to offer a leading role in identifying and solving pressing environmental problems (Worster 1994; Lubchenco et al. 1991; Levin 1999; Ludwig, Mangel, and Haddad 2001). There is a huge premium, then, to resolve complexity in ways that enable one to make general predictions about how ecosystems will function in response to myriad natural and human-caused disturbances. Making reliable predictions requires having a solid empirical understanding of how the components fit together to determine whole ecosystem functioning. In this endeavor, ecologists must, to some extent, embrace ecological details because they provide the contexts for discovering the mechanisms leading to different outcomes. The challenge, then, is to develop an empirical research program that can resolve what mechanisms must be understood

in order to predict the different outcomes (Levin 1992). This book elaborates such an empirical program.

## PHILOSOPHICAL MUSINGS

Ecologists do not rely on a single empirical method to derive understanding of their systems (Hairston 1990). Broadly speaking, they use two different kinds of approaches: experimentation (Hairston 1990) and meta-analyses (Peters 1986; Hedges, Gurevitch, and Curtis 1999; Osenberg, Sarnelle, and Cooper 1999). Experimentation is believed to lead to predictive insights because it uncovers causal relationships (Lehman 1986). Meta-analysis is believed to offer predictive insights whenever the function that is statistically fit to the data explains a good degree of variation in the data set (Peters 1986). These different approaches lead to different understanding of the relationship between the whole system and its component parts and ultimately on the application of that knowledge to solve environmental problems (Lehman 1986; Lawton 1999). Let me illustrate my point with an example.

Suppose we agreed that a reasonable way to characterize ecosystems is by their component plant species and the plant species' trophic linkages with the soil nutrient pool. Suppose that ultimately we wanted to predict how the number of plant species (a measure of plant species diversity) influenced the level of some ecosystem function such as nutrient cycling or primary production. We might then manipulate plant species diversity in a single location and measure the ensuing levels of ecosystem function. Let's further suppose that this experimental protocol was used to evaluate the relationship between plant species diversity and ecosystem function across geographic locations. Such coordinated research could, and indeed often does, reveal different functional relationships in different locations (figure 1.1). At some locations, there could be strong positive relationships between plant species diversity and ecosystem function, as revealed by the steep slope of the regression line. At other locations, flat, almost horizontal lines infer weak if any relationships. Finally, at other locations there could be negative relationships between plant species diversity and function. This leads to a dilemma because we don't know which causal relation to use when making predictions about ecosystem responses to, say, loss of species diversity.

Such an outcome has led to despair that results from experimental ecology are insufficient to make general predictions because the outcomes are entirely context dependent. It is argued that experimentation will never uncover the suite of variables needed to make reliable predictions for all local conditions
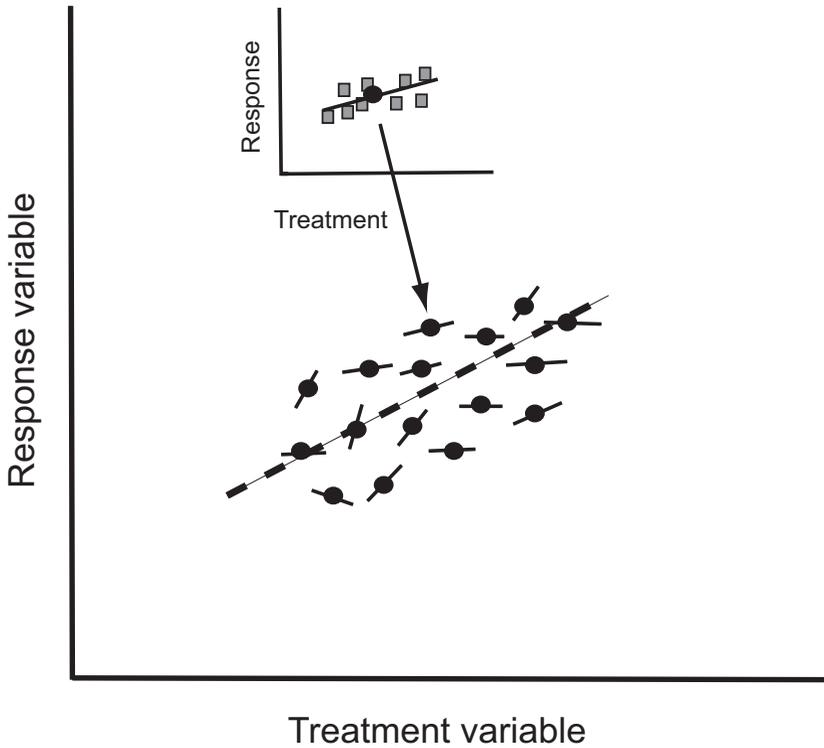
FIGURE 1.1. Hypothetical case in which the relationship between a treatment and response variable is deduced by identifying an average trend (dashed line) among data compiled from numerous, local experiments. The circles represent the mean response magnitude for a given experiment at a particular local site. The solid lines through the circles represent the slope of the causal relationship between treatment and response variable measured in each local experiment (see inset). The figure illustrates that the deduced average trend in the metadata may not identify the correct causal relationship owing to local contingency in the way that the treatment variable is manifest as a response. This figure illustrates that general predictions for science and management cannot necessarily be made using trends derived from metadata.

(Lawton 1999). Instead, it is believed that predictive ability is more likely to come about by combining data from the many study sites and estimating the degree of statistical association between variables of interest (Peters 1986; Lawton 1999). The problem here is that one derives an association, not a causal insight, and so it is merely a "rough" generalization (figure 1.1). Moreover, it is not a meaningful generalization because it abstracts the contingent outcomes among locations. There is no guarantee that, say, boosting plant diversity at

any one location will enhance ecosystem function, even though the rough generalization says it ought to. This example illustrates that neither experimental nor meta-analytic approaches necessarily produce predictive insights that can be applied to management if they do not explicitly confront the issue of *contingency*.

Contingency arises when the nature and strength of ecosystem functioning in different locations are different realizations of the same underlying process. I show in this book how focusing empirical research to explain contingent outcomes can lead to predictive understanding of ecosystem function.

## EXPLAINING CONTINGENCY: A WORLDVIEW

I am certainly not the first to suggest that focusing on contingency may help to resolve ecosystem complexity. Both Schoener (1986b) and Simberloff (2004) propose ways to gain understanding of contingency. One way might be to treat contingencies as important case studies, each with their own rich ecological detail (Simberloff 2004). By amassing collections of these case studies one might identify a set of common properties that can guide environmental problem solving and lead to approximate generalizations (Simberloff 2004; see also Shrader-Frechette and McCoy 1993). Another way might be to identify a set of primitive properties or axes representing organismal traits (e.g., species body size distributions, life-cycle characteristics, mobility) and environmental conditions (e.g., environmental severity, trophic structure, resource inputs) and then ordinate systems along the axes (Schoener 1986b). The intent here is to provide some rational ordering of contingency based on fundamental ecological details.

The limitation of both these approaches, as I see it, is that they do not offer a set of rules that enables one to predict how a collection of species with a given set of traits living under a specific set of environmental conditions might fare if they were placed into a new set of environmental conditions. That is, they describe what exists under current environmental conditions but they do not offer a means to predict what may happen as environmental conditions change.

The alternative approach that I present in this book follows from a worldview that—to paraphrase Hutchinson (1965)—considers ecological systems as theaters in which evolutionary ecological acts play themselves out. Such a perspective recognizes that the acts will play themselves out differently in different ecological contexts (theaters), even with identical sets of actors (individuals or species). That is, the act itself is not scripted; it is an improvisation that

unfolds differently in different theaters. What this implies is that contingency comes about because of emergent properties of a system; it is a manifestation of the way the act plays itself out in a local theater. To explain contingent outcomes, then, requires understanding the ground rules for the improvisation. This means identifying fundamental rules or fundamental mechanisms, mechanisms that are evident among all systems regardless of spatial extend and temporal scale (Dunham and Beaupre 1998; Petersen et al. 2003; Schmitz 2005b).

Identifying fundamental mechanisms requires identifying ultimate rather than proximate causes of ecological processes that lead to variation across space and time (Mayr 1982). Ultimate explanations, in turn, need to consider the evolutionary ecology of species that comprise ecosystems in order to explain function. This need to link evolutionary and ecosystem ecology to improve prediction has been recognized for some time (Lehman 1986; Oksanen 1988; Levin 1992; Holt 1995; Carpenter and Turner 2000). But, it has been challenging to make the link empirically operational.

To address this challenge, I begin with the universal conception (Paine 1988; Tilman 1989; Cohen, Briand, and Newman 1990) that ecosystems are comprised of species that consume resources and that those consumer species are, in turn, resources for other consumers. From this conception, one can deduce a fundamental rule or mechanism for enacting the play. That is, individuals within a species ought to exhibit flexible adaptive responses to balance fitness gains from foraging against fitness losses related to decreasing the risk of being consumed (Sih 1980; Mangel and Clark 1988; Lima and Dill 1990; Holt 1995; Lima 1998). This fundamental mechanism can transcend spatial and temporal scales, and taxa, but the exact way that the trade-off is balanced will depend on local ecological context (Schmitz 2005b). I illustrate throughout this book how such a fundamental conception has far-reaching implications for explaining the rich ways that consumer-resource (trophic) interactions play themselves out in ecosystems.

## CONTINGENCY AND EMERGENCE

By invoking the idea that contingency is an emergent property of ecosystems, I distinguish between weak and strong emergence (Polkinghorne 2005). Weak emergence arises when a whole system property or function emerges as a consequence of causal interactions at a lower level of organization (Polkinghorne 2005). Schoener's (1986b) attempt to synthesize ecological contingency using a suite of basic organismal traits and environmental conditions to characterize system types is an example of the application of the principle of weak emer-

gence. Strong emergence would arise if a new set of causal principles became active in a complex system (Polkinghorne 2005). Strong emergence has been invoked, for example, in explanations of how over the course of the history of life, primitive, competing microorganisms coalesced and forged new synergistic relationships that led to their collective persistence and reproduction—the emergence of individuality (Buss 1987).

Ecologists too have entertained the possibility that ecosystem structure and function is the consequence of strong emergence. Ecology, as originally conceived, focused on individuals of species and their interactions with members of other species and the environment, to build upon the Darwinian view of nature (Haeckel 1866). But, that individual organismic view gave way to studying the properties of ensembles of species as an individual entity—a homeostatic community. This eventually led to the view that species acted synergistically to maintain the structure and function of the whole community, in much the same way that organs in a body contribute to the structure and function of the organism as a whole—the Clementsian view (Clements 1916) of ecological systems (Shrader-Frechette and McCoy 1993; Worster 1994). Tansley (1935) offered forceful and persuasive arguments against this view. The argument held that communities could not be typecast as individuals because the traits and the development processes that gave them their putatively individual character—their species composition—changed among ecological settings, and so they did not remain as homoeostatic entities in space and time.

The distinction between weak and strong emergence also helps to put into some context the ecological maxim that "the whole is greater than the sum of the parts." Many ecologists interpret this to mean that prediction is extremely difficult if not impossible because nonlinearities (nonadditive effects) cause emergent properties that cannot ever be understood by figuring out how the component parts fit together—a strong emergence view. But, consider Tansley's (1935) take on this issue: "I do think a good deal of fuss is being made about very little. . . . What we *observe* is juxtaposition and interaction, with the resulting emergence of what we call . . . a 'new' entity. And who will be so bold as to say that this new entity, for example the molecule of water and its qualities, would be unpredictable, if we really understood all the properties of hydrogen and oxygen atoms and the forces brought into play in their union? Unpredictable by us with our present knowledge, yes: but theoretically unpredictable, surely not." Tansley essentially argues that we should resist the tendency to invoke strong emergence simply because we do not yet have a good mechanistic understanding of system structure and functioning. That is, the component parts may produce nonadditive outcomes, but those outcomes may still be predictable once we obtain a mechanistic understanding of the way the

components interact to produce an effect (e.g., see chapter 6). I use the term *mechanistic understanding* here in the spirit of Schoener (1986a) and Dunham and Beaupre (1998) to mean the appropriate level of reductionism needed to provide a causal understanding of functional relationships. The crux of the issue here is not that additivity and nonadditivity cause different predictive ability. Rather, it is understanding why the mechanisms of interaction under different contexts lead to additive or nonadditive effects.


## PREPARING THE MIND FOR DISCOVERY

Finding the appropriate level of reductionism requires taking the altogether holistic view that ecology is a single discipline that integrates principles from various subfields, including evolutionary, population, community, and ecosystem ecology (Tilman 1989; Levin 1992). It also requires that we actively intertwine theory and empiricism (Kareiva 1989), but not simply for purposes of explicitly testing formal theoretical predictions. Rather, an important value of theory is that it leads to a priori expectations—deductions—that "prepare the mind" (Power, Dietrich, and Sullivan 1998; see also Roughgarden, May, and Levin 1989) to notice phenomena that we otherwise might not if we relied on simple intuition alone.

For example, during the course of testing prevailing theory on trophic interactions (Oksanen et al. 1981) in an old-field ecosystem in Connecticut, I noticed that the species of spider predator used in experiments did not have a net direct effect on the density of its grasshopper prey. Nevertheless, there seemed to be indirect effects on the grasshoppers' resources (a positive indirect effect on grasses and a negative indirect effect on herb). These observations were completely at odds with the theory. However, I was also acquainted with two bodies of theory that held that predators should cause prey to respond behaviorally to avoid predation risk (Sih 1980; Mangel and Clark 1988; Lima and Dill 1990) and that such behavior could have profound effects (Abrams 1984; and perhaps counterintuitive effects [Abrams 1992]) on trophic interactions in food chains. Drawing upon the deductions made by this body of theory, my research group and I were eventually able to resolve the behavioral-ecological process—grasshopper habitat shift from nutritious but risky grasses to safe but less nutritious herbs to avoid predation risk—that caused the emergent indirect effects at the food chain level (Beckerman, Uriarte, and Schmitz 1997; Rothley, Schmitz, and Cohon 1997; Schmitz, Beckerman, and O'Brien 1997). This key discovery then opened the door to develop a systematic, integrated understanding of the structure and functioning of this ecosystem (Schmitz 2004,

2006, 2008; Schmitz, Kalies, and Booth 2006). Stumbling on this discovery and the ensuing insight it provided could be considered a lucky break. In some sense this may be true given that the behaviorally mediated effects did not occur in two other geographic locations involving species of spider predators, grasshopper herbivores, and grass and herb resources that were similar to the Connecticut system (Schmitz 1993, 1994). But, we also "made" our own luck by being prepared to notice the anomalous outcome and offer a mechanistic explanation for it, rather than dismiss it as a failed experiment.

In preparing the mind with theory, one must be careful, however, to keep a critical but open mind (Brown 2001) and let Nature speak for itself. Sometimes, preparing the mind with theory can lead to preconceived notions of what Nature should look like. We then end up trying to fit Nature to the theory. The point is that observing Nature—the enterprise of natural history, even if conducted in a systematic, deductive way—is fundamental to developing reliable explanations of why Nature works the way it does (Power, Dietrich, and Sullivan 1998). Here, theory has its greatest value if it guides us toward discovering explanations for observed phenomena. In other words, don't speak to Nature but let Nature speak to you.

## STRUCTURE OF THE BOOK

My experience conducting empirical research in a variety of locations and ecosystem types has caused me to wonder why there were differences in the nature and strength of the trophic interactions in ecosystems in different geographic locations despite much similarity in their components. This book presents my answers to this question. But, in writing it, I do not intend simply to provide answers, nor suggest that I have all the answers. Rather, the larger objective of the book is to relate to the reader a process I have found useful in my efforts to derive a causal understanding of ecological contingency and hence to resolve ecological complexity.

This book attempts to explain how biotic interactions that determine the nature and strength of trophic interactions and dynamics of species in ecological food webs—the domain of community ecology—influence biophysical properties (e.g., organic matter pool content, soil elemental content, trophic structure, trophic transfer efficiencies) and functions (or processes) such as production, decomposition, and elemental cycling—the domain of ecosystem ecology.

There is much interest in reconnecting these dichotomous approaches given the recognition that biotic interactions among species (as a consequence of

their traits and functional roles) may be important mediators of biophysical properties and functions (Chapin et al. 1997, 2000; Hooper et al. 2005). Moreover, concern over risks that attendant changes in species composition will alter ecosystem properties and functions has led to increased interest in developing a predictive theory for ecosystem dynamics that considers the explicit dynamical interplay among the biotic and biophysical components of ecosystems (Levin 1992; Chapin et al. 1997, 2000; Carpenter and Turner 2000).

This book is structured around using reductionism to answer several questions, such as: How do we conceptualize and ecosystem in ways that blend biotic and biophysical components of ecosystems? How do we scale individual-level processes to ecosystem-level processes? When are trophic interactions in ecosystems controlled by top-down and bottom-up processes? What determines the sign and strength of indirect effects in ecosystems? How do we develop an understanding of the relationship between functional biotic diversity of ecosystems and ecosystem properties and functions? How do we scale basic scientific insights derived from detailed, local, small-plot field experiments to applied management questions on landscape scales? How do we use evolutionary ecological principles to derive an operational understanding of complex, adaptive ecosystems? These are critical questions that contemporary ecology struggles to answer. It is my hope that the book will offer the reader operational ways with which to pursue answers to these questions and thereby help foster the transition of ecological science from a field that is largely struggling to understand complexity to a field that can make reliable predictions about the emergence of contingent outcomes in nature.